The Genus *Amarophos* Woodring, 1964 (Gastropoda: Buccinoidea) in the Tropical American Neogene, with a Description of Two New Species

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Abstract. The presence of the extinct buccinid genus *Amarophos* in the tropical American Caribbean Neogene is reviewed with the description of two new Lower Pliocene species: *Amarophos woodringi* nov. sp. from the Shark Hole Point Formation of the Bocas del Toro region, Panama; and *Amarophos arayaensis* nov. sp. from the Aramina Formation of the Araya Peninsula, Venezuela. These new records extend both the previously known geographical and geological distribution of the genus.

INTRODUCTION

The genus Amarophos was described by Woodring (1964) based on fossil material from the Lower Pliocene Chagres Formation of Panama (now considered Messinian, uppermost Miocene; Coates et al., 2005: fig. 9). In the generic description, Woodring (1964) argued that Amarophos was closely similar in outline to Rhipophos Woodring, 1964, described from the Upper Miocene Middle and Upper Gatun Formations of Panama, but with a wider and more channelled suture. In Amarophos, the ribs on the later teleoconch whorls are obsolete or almost so, and if present they are crowded and poorly delimited, so that the spiral sculpture is always predominant on the last whorl. In Rhipophos, the axial ribs also are crowded, but they persist on the last whorl and are more or less equal in strength to the spiral cords, giving the last whorl a finely cancellate appearance.

Woodring considered *Ptychosalpynx? dentalis* Olsson, 1922 from the then Lower Miocene Uscari Shale of Costa Rica the earliest member of the genus and stated that it is a very typical shell for the Upper Uscari Formation. The uppermost Uscari Formation is now considered to be Tortonian-Messinian in age by Coates et al. (2005: fig. 9). Woodring (1964) also reported that Olsson had collected *Anuarophos dentalis* from the Lower Miocene Las Perdices Shale of Colombia (Olsson, personal communication in Woodring, 1964).

These deposits are now considered upper Middle to Upper Miocene (Duque-Caro, 1990). Taking into account the recalibration of the age of the assemblages, until now *Anarophos* was known only from the Upper Miocene.

In this paper, two additional members for the genus are described, both from the Lower Pliocene: one species from the Shark Hole Point Formation of the Valiente Peninsula (Bocas del Toro region), Panama, and the other species from the Aramina Formation, Araya Peninsula (Sucre), Venezuela.

MATERIALS AND METHODS

This work includes previously known museum fossil material present in the Panama Palaeontological Project collections (Naturhistorisches Museum Basel [NMB], Switzerland) and newly collected specimens resulting from extensive fieldwork undertaken by us in the Caribbean Neogene Formations of Panama and Venezuela during the past 10 yr.

The material from the Shark Hole Point comes from the east coast of the Valiente Peninsula, Bocas del Toro region, Panama (Figure 1). Coates et al. (2005) review the stratigraphy of the Neogene rocks of the Bocas del Toro region, and they dated the Shark Hole Point Formation as Lower Pliocene (5.3–3.6 Ma). Benthic foraminifera indicate that the paleobathymetry ranged

Page 103

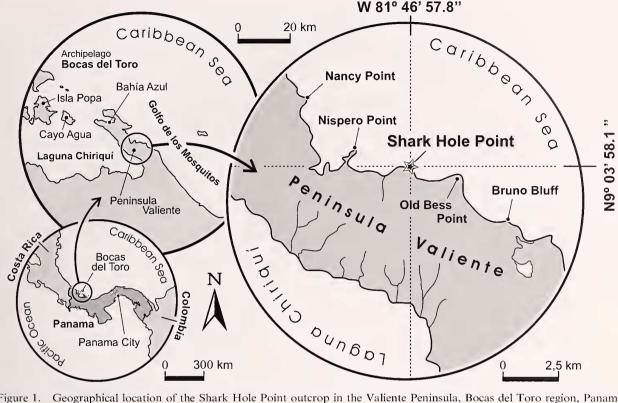


Figure 1. Geographical location of the Shark Hole Point outcrop in the Valiente Peninsula, Bocas del Toro region, Panama.

from -100 to -200 m (Collins, 1993). For further information, see Coates et al. (2005).

The material from Cerro Barrigón comes from the Araya Peninsula, Sucre, mainland Venezuela (Figure 2). Macsotay & Hernandez (2005) considered the sedimentary sequence at Cerro Barrigón to correspond to the Aramina Formation, Cubagua Group, Lower Pliocene. For further information, see Landau and Da Silva (2010).

The material described and discussed here is housed in the Naturhistorisches Museum Basel (NHB collection [coll.]), Switzerland, and in the Bernard Landau collection to be housed in the Naturhistorisches Museum Wien (NHMW coll.), Vienna, Austria. Type material is deposited in the Naturhistorisches Museum Wien (NHMW coll.), Vienna, Austria.

In the Systematic Palaeontology section, we have followed the classification proposed by Bouchet & Rocroi (2005).

SYSTEMATIC PALAEONTOLOGY

BUCCINOIDEA Rafinesque, 1815

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Pisaniinae Gray, 1857

Traditionally, the sand-dwelling "Phos" group of taxa have been placed in the Photinae Gray 1857, synonymized with Pisaniinae Gray, 1857 by Bouchet & Rocroi (2005:255). This position was followed by Watters (2009) in his revision of several pisinine genera in the Recent western Atlantic. This may not be correct, and molecular data are needed to confirm this synonymy (Vermeij, personal communication).

Genus Amarophos Iredale, 1921

Type species: By original designation, Amarophos bothrus Woodring, 1964: 267. Fossil, Neogene Caribbean.

Amarophos woodringi nov. sp.

(Figures 3-11)

Dimensions and type material: Holotype NHMW 2010/ 0176/0001 (Figures 1-3), height 25.2 mm, maximum width 16.7 mm; paratype 1 NHMW 2010/0176/0002 (Figures 4-6), height 25.0 mm; paratype 2 NHMW 2010/0176/0003 (Figures 7-9), height 30.7 mm (NHMW coll., ex BL coll.).

Etymology: Named in honour of Wendell Phillips Woodring, in recognition of his enormous contribution to Caribbean Neogene malacology during his work with the U.S. Geological Survey (USGS).

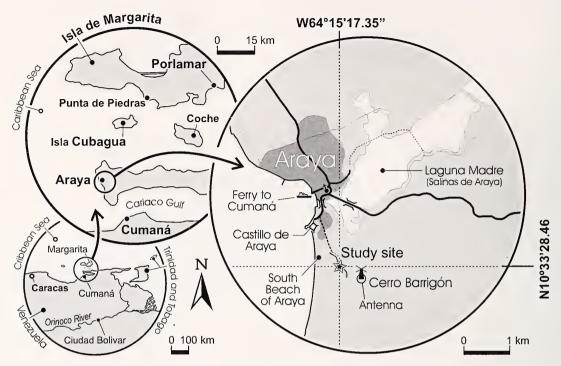


Figure 2. Geographical location of the Araya Peninsula outcrop in the Araya Peninsula, Sucre, Venezuela.

Type locality: Shark Hole Point, Valiente Peninsula, Bocas del Toro region, Panama.

Stratum typicum: Shark Hole Point Formation, Lower Pliocene.

Additional material: Fourteen specimens, Shark Hole Point Formation, Shark Hole Point, Valiente Peninsula, Bocas del Toro region, Panama. (BL coll./ NHMW coll.).

Locality PPP00386 (NMB17854), 10 specimens, unnumbered lot; PPP00388 (NMB17855), four specimens, unnumbered lot; PPP00390 (NMB17856), six specimens, unnumbered lot; locality PPP00392 (NMB17857), two specimens, unnumbered lot; locality PPP00391 (NMB17858), five specimens, unnumbered lot; locality PPP00396 (NMB17908), one specimen, unnumbered lot; locality PPP00397 (NMB17859), 47 specimens, unnumbered lot; locality PPP00400 (NMB17860), eight specimens, unnumbered lot; locality PPP01293 (NMB18545), seven specimens, unnumbered lot; locality PPP01714 (NMB18768), four specimens, unnumbered lot; locality PPP02189 (NMB18688), 35 specimens, unnumbered lot; locality PPP02191 (NMB18690), seven specimens, unnumbered lot; locality PPP02190 (NMB18689), one specimen, unnumbered lot; seven specimens, unnumbered lot; locality PPP02195 (NMB18694), 11 specimens, unnumbered lot; locality PPP02196 (NMB18695), seven specimens, unnumbered lot; locality PPP02197 (NMB18696), 18 specimens, unnumbered lot; locality PPP02198 (NMB18697), 21 specimens, unnumbered lot; locality PPP02199 (NMB18698), one specimen, unnumbered lot; locality PPP02200 (NMB18699), one specimen, unnumbered lot; locality PPP02201 (NMB18700), nine specimens, unnumbered lot; locality PPP02202 (NMB18701), 12 specimens, unnumbered lot; locality PPP02203 (NMB18702), one specimen, unnumbered lot; locality PPP02204 (NMB18703), 16 specimens, unnumbered lot; locality PPP02227 (NMB18724), five specimens, unnumbered lot; locality PPP02229 (NMB18726), 17 specimens, unnumbered lot.

Diagnosis: A small- to medium-sized *Amarophos* species, with a relatively narrow canaliculate suture, convex spire whorls, inflated-ovate last whorl, and a very fine reticulate sculpture on later teleoconch whorls, with the spiral component predominant, finely beaded.

Description: Shell small- to medium-sized for genus, relatively solid, ovate with a scalate spire. Protoconch and early teleoconch whorls decorticated in all specimens. Teleoconch consists of five to six convex whorls, with the periphery at the abapical suture. Suture deeply canaliculate, forming a narrow infrasutural gutter, widening slightly abapically. Third teleoconch whorl (first teleoconch whorl with surface ornament preserved) bears 11–13 narrow, elevated, widely spaced axial ribs and five or six narrow, close-set spiral cords. A secondary spiral thread or cord is

developed in the interspaces, variable in strength and onset. Abapically the axial ribs weaken, obsolete on the penultimate and last whorl, where the axial sculpture consists of sharp, close-set growth lines giving the surface a finely reticulate appearance. At the intersections where the spiral cords override the axial growth lines, the cords are lightly thickened, giving them a finely beaded appearance. Penultimate whorl with five to six spiral cords. Last whorl inflated, ovate, widely convex in profile, constricted at the base, bearing 16-19 narrow, elevated spiral cords. Aperture small- to medium-sized, ovate. Outer lip sinuous in profile, with a pronounced notch abapically; lip edge sharp, crenulated; lip callus absent; aperture strongly and deeply lirate within, 13-15 well-developed lirae that stop just short of the lip edge; anal canal poorly developed, marked by a shallow groove; siphonal canal open, relatively long, narrow, strongly posteriorly recurved. Columella deeply excavated in the midportion, with a strong columellar fold at its abapical edge bordering the siphonal canal and five or six weaker tubercles or folds above the terminal columellar fold, weakening adapically, developed to a variable degree. Columellar callus hardly developed, the spiral sculpture visible through the very fine callus wash. Siphonal fasciole somewhat swollen, sculptured by spiral cords.

Discussion: Amarophos woodringi nov. sp. is relatively common in the Pliocene clays of Shark Hole Point, Panama. The shells are fairly uniform in shape and height of spire, but they vary in size, measuring from 20.3 to 30.8 mm in height. The most variable shell feature is the strength of the secondary spiral cords and the position at which they first appear. In the holotype, the secondary threads only appear on the last whorl and remain very weak, whereas is other specimens they appear as early as the fourth teleoconch whorl and are only slightly weaker than the primary spiral cords. The strength and number of columellar folds or tubercles developed above the abapical columellar fold is also highly variable. Unfortunately, the protoconch and early teleoconch whorls are decorticated or missing in all the specimens available. Interestingly, Woodring (1964) made the same observation for his specimens of Amarophos bothrus Woodring, 1964 from the Chagres Formation of Panama.

Woodring (1964:267) mentioned the presence of an undescribed *Amarophos* species in "strata of late Miocene age in the Bocas del Toro area of northwestern Panamá (USGS 8322, Valiente Peninsula)." He was undoubtedly referring to this species, a common species at Shark Hole Point.

Amarophos bothrus Woodring, 1964 (Figures 12, 13, holotype; Figures 14–19, additional specimens) from the Chagres Formation of Panama was considered to

be Lower Pliocene by Woodring (1964) but is now known to be Messinian, uppermost Miocene (Collins et al., 2005:fig. 9; 5.8–6.2 Ma). Woodring (1964) distinguished *A. bothrus* from the then undescribed Valiente Peninsula species as being smaller and more slender. Size may not be a reliable feature by which to separate the two taxa, because many shells of *A. woodringi* are smaller than the size given for *A. bothrus* (24.7 mm in height). *Amarophos woodringi* has a more ovate, slightly more inflated and squatter shell, the spire whorls are more convex, the last whorl more inflated, less elongate and slightly more strongly constricted at the base, and the primary spiral cords are sharper and narrower than in *A. bothrus*.

Amarophos dentalis (Olsson, 1922; Figures 20, 21) from the Tortonian-Messinian Miocene of Atlantic Costa Rica differs from *A. woodringi* in having a taller, more regularly conical spire; a narrower and less strongly developed sutural gutter; a more rounded last whorl adapically; and axial ribs that persist, albeit weakly, onto the last whorl, whereas there are no ribs on the last whorl of *A. dentalis*.

Amarophos arayaensis nov. sp.

(Figures 22-24)

Dimensions and type material: Holotype NHMW 2010/ 0176/0004 (Figures 22–24), height 41.2 mm, width 20.7 mm (NHMW coll., ex BL coll.).

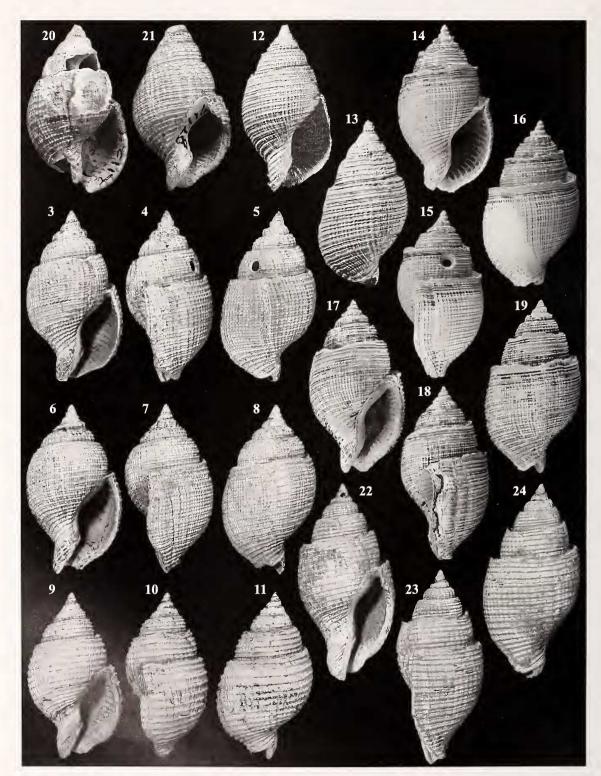
Etymology: Named after the type locality, Araya Peninsula.

Type locality: Upper reddish coarse sandy bed, Cerro Barrigón, Araya Peninsula (of Landau & Silva, 2010), Venezuela.

Stratum typicum: Aramina Formation, Cubagua Group, Lower Pliocene.

Diagnosis: A large *Amarophos* species, with a very wide infrasutural gutter, barrel-shaped last whorl, relatively numerous axial ribs on the early teleoconch whorls, relatively numerous spiral cords on the penultimate whorl, elongated aperture, siphonal canal hardly posteriorly recurved, narrowly excavated columella and thick columellar callus for genus.

Description: Shell large for genus, relatively solid, barrel-shaped last whorl, scalate spire. Protoconch and early teleoconch whorls decorticated. Teleoconch consists of seven convex whorls, with the periphery at the abapical suture. Suture deeply canaliculate, forming a wide, slightly concave to flat-bottomed, infrasutural gutter. Fourth teleoconch whorl (first teleoconch whorl with surface ornament well pre-



Figures 3–5. *Amarophos woodringi* nov. sp. Holotype NHMW 2010/0176/0001 (NHMW coll., ex BL coll.). Height 25.2 mm. Shark Hole Point Formation, Lower Pliocene, Shark Hole Point, Valiente Peninsula, Bocas del Toro region, Panama. Figures 6–8. *Amarophos woodringi* nov. sp. Paratype 1 NHMW 2010/0176/0002 (NHMW coll., ex BL coll.). Height 25.0 mm. Shark Hole Point Formation, Lower Pliocene, Shark Hole Point, Valiente Peninsula, Bocas del Toro Region, Panama.

served) bears 16 rounded, prosocline axial ribs and eight narrow, close-set spiral cords. A secondary and sometimes tertiary spiral thread is developed in the interspaces on the penultimate and last whorls. Abapically the axial ribs weaken, subobsolete on second half of the fourth whorl. On the second half of the penultimate whorl and last whorl the axial sculpture reappears, consisting of narrow, poorly defined, very close-spaced, flattened ribs. The spiral cords overrun the indistinct ribs giving them a finely wavy appearance. At the sculptural intersections, the cords are lightly thickened, giving them a very weakly beaded appearance. Penultimate whorl with nine spiral cords. Last whorl barrel-shaped, weakly convex in profile, with a wide infrasutural gutter, weakly constricted at the base, bearing 18 narrow spiral cords. Aperture small- to medium-sized, elongate-ovate. Outer lip edge missing: lip callus absent; aperture strongly and deeply lirate, with 16 lirae within; anal canal clearly developed, represented by narrow groove; siphonal canal open, relatively long, narrow, weakly posteriorly recurved. Columella moderately excavated in the mid-portion, with a strong columellar fold at its abapical edge and indistinct tubercles or folds running along the entire outer columellar margin, two elongated folds in the parietal region extending deep within the aperture. Columellar callus thickened, well-delimited, narrowly expanded. Siphonal fasciole sculptured by spiral cords.

DISCUSSION

Although represented by a single specimen, *Amarophos arayaensis* nov. sp. is quite different from all its congeners in having a much larger, more barrel-shaped shell, with a much wider infrasutural gutter. It also has more numerous and less widely spaced axial ribs on the early teleoconch whorls, more numerous spiral cords on the penultimate whorl, and the last whorl is more elongated and far less constricted at the base. The siphonal canal is less strongly posteriorly recurved, the columella is less excavated in the mid-portion, thicker, and with more tubercles or folds along its edge.

Amarophos arayaensis is most similar in shape to Amarophos bothrus Woodring, 1964 from the Chagres Formation of Panama, but with a shell twice the size. They differ mainly in the character of the last whorl that is even more elongated and less constricted at the base than in A. arayaensis. The infrasutural gutter is wider in A. arayaensis, the siphonal canal is straighter, less recurved; the columella is less excavated and the columellar callus is thicker. Amarophos dentalis (Olsson, 1922) is quite different, with a more conical spire, a much narrower sutural gutter, and a more rounded last whorl. Of all the Amarophos species A. dentalis has the most strongly developed axial sculpture. Although always weakly developed in the genus, narrow elevated axial ribs are present on the last whorl of A. dentalis, whereas both the penultimate and last whorls in A. arayaensis have closely crowded axial lamellae but no elevated ribs.

Paleobiological implications: With the descriptions of A. woodringi nov. sp. and A. arayaensis nov. sp., the known number of members of this genus is doubled to four. Amarophos is an unusual genus in the Caribbean Neogene, because it seems to have been quite restricted in both its geographical and geological distribution. The genus has so far been found only in the Atlantic portion of the Gatunian palaeobiogeographical province (sensu Vermeij & Petuch 1986; Landau et al. 2008), and even here it is restricted to the Central Americannorthern South American Subprovince (of Woodring, 1974; =Limonian Subprovince of Petuch, 1988) and the Colombian-Venezuelan-Trinidad Subprovince (of Woodring, 1974; =Puntagavilanian Subprovince of Petuch, 1988). The faunal province names used herein are those erected by Woodring (1974) and are preferred over those proposed by Petuch (1988; but see Landau

Figures 9–11. Amarophos woodringi nov. sp. Paratype 2 NHMW 2010/0176/0003 (NHMW coll., ex BL coll.). Height 30.7 mm. Shark Hole Point Formation, Lower Pliocene, Shark Hole Point, Valiente Peninsula, Bocas del Toro region, Panama.

Figures 12–13. *Amarophos bothrus* Woodring, 1964. Holotype USNM 643697. Height 24.7 mm. upper Chagres Formation, Messinian, Upper Miocene, locality 208 (of Woodring, 1964) Mouth of Rio Indios, Panama (reproduced from Woodring, 1964: pl. 47, figs. 1, 2).

Figures 14–16. *Amarophos bothrus* Woodring, 1964. NMB H19489. Height 28.9 mm. Upper Chagres Formation, Messinian, Upper Miocene, locality NMB 18990, Colón. North coast, west of Colón. Approximately 4.4-km air distance west of Río Indio and approximately 900 m east of Punta Gavilán, Morro Rajado.

Figures 17–19. *Amarophos bothrus* Woodring, 1964. NMB H19490. Height 31.1 mm. Upper Chagres Formation, Messinian, Upper Miocene, locality NMB 18990, Colón. North coast, west of Colón. Approximately 4.4-km air distance west of Río Indio and approximately 900 m east of Punta Gavilán, Morro Rajado.

Figure 20. Amarophos dentalis Olsson, 1922. Syntype PRI 21124. Height 29.0 mm. uppermost Uscari Formation, Tortonian-Messinian, Upper Miocene, Cocles Creek, Limon Costa Rica (Olsson, 1922: specimen pl. 15, fig. 14).

Figure 21. Amarophos dentalis Olsson, 1922. Syntype PRI 21128. Height 27.3 mm. uppermost Uscari Formation, Tortonian-Messinian, Upper Miocene, Cocles Creek, Limon Costa Rica (Olsson, 1922: specimen pl. 15, fig. 18).

Figures 22–24. *Amarophos arayaensis* nov. sp. Holotype NHMW 2010/0176/0004 (NHMW coll., ex BL coll.). Height 41.2 mm. Aramina Formation, Cubagua Group, Lower Pliocene, Upper reddish coarse sandy bed, Cerro Barrigón, Araya Peninsula.

et al., 2008). Geologically, the previous records of the genus are restricted to the Tortonian-Messinian, Upper Miocene (*A. dentalis* and *A. bothrus*). These new records extend the known range into the Lower Pliocene (*A. woodringi* and *A. arayaensis*). There is no further record for the genus.

The origin of *Amarophos* is obscure. Woodring (1964) suggested it might have evolved from *Rhipophos* Woodring, 1964 that occurs in the Upper Miocene Middle and Upper Gatun Formations of Panama but pointed out such a lineage was not possible because they were considered coeval at the time. With the recalibration of the age of many of the Caribbean assemblages, *Amarophos* is indeed slightly younger, with a first appearance in the Tortonian-Messinian rather than the Serravalian-Tortonian for *Rhipophos*. However, in our opinion this lineage is conjectural. Unfortunately, the protoconch that has been used as an important generic character in the *Phos* group of buccinids (i.e. Olsson, 1964) is missing in all *Amarophos* specimens examined.

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LITERATURE CITED

- BOUCHET, P. & J. P. ROCROI. 2005. Classification and nomenclator of gastropod families. Malacologia 47(1–2): 1–397.
- COATES, A. G., D. F. MCNEILL, M. P. AUBRY, W. A. BERGGREN & L. S. COLLINS. 2005. An introduction to the

Geology of the Bocas del Toro Archipelago, Panama. Caribbean Journal of Science 41(3):374–391.

- COLLINS, L. S. 1993. Neogene paleoenvironments of the Bocas del Toro Basin, Panama. Journal of Paleontology 67:699– 710.
- DUQUE-CARO, H. 1990. Neogene stratigraphy, paleoceanography and palaeobiogeography in northwest South America and the evolution of the Panama seaway. Palaeogeography, Palaeoclimatology, Palaeoecology 77(3-4):203–234.
- LANDAU, B. M. & C. M. DA SILVA. 2010. Early Pliocene gastropods of Cubagua, Venezuela: taxonomy, palaeobiogeography and ecostratigraphy. Palaeontos 19:1– 221.
- LANDAU, B. M., G. J. VERMEIJ & C. M. DA SILVA. 2008. Southern Caribbean Neogene palaeobiogeography revisited. New data from the Pliocene of Cubagua, Venezuela. Palaeogeography, Palaeoclimatology, Palaeoecology 257: 445-461.
- MACSOTAY, O. & R. C. HERNANDEZ. 2005. Paleoclimatology of the Pleistocene-Holocene using marine molluscs and hermatypic corals from northern Venezuela. Transactions of the 16th Caribbean Geological Conference, Barbados. Caribbean Journal of Earth Science 39:93–104.
- OLSSON, A. A. 1964. Neogene mollusks from northwestern Ecuador.. Paleontological Research Institution: Ithaca, New York. 256 pp.
- PETUCH, E. J. 1988. Neogene history of tropical American mollusks. Biogeography and evolutionary patterns of tropical western Atlantic Mollusca. Coastal Education and Research Foundation: Charlottesville, Virginia. 217 pp.
- VERMEIJ, G. J. & E. J. PETUCH. 1986. Differential extinction in tropical American molluscs: endemism, architecture, and the Panama land bridge. Malacologia 27:29–41.
- WATTERS, G. T. 2009. A revision of the western Atlantic Ocean genera Anna, Antillophos, Bailya, Caducifer, Monostiolum, and Parviphos, with description of a new genus Dianthiphos, and notes on Engina and Hesperisternia (Gastropoda: Buccinidae: Pisaniinae) and Cumia (Colubrariidae). The Nautilus 123:225–275.
- WOODRING, W. P. 1964. Geology & paleontology of the Canal Zone and adjoining parts of Panama. Geology and description of the Tertiary Mollusks (Gastropods: Columbellidae to Volutidae). U.S. Geological Survey Professional paper 306-C, 241–297.
- WOODRING, W. P. 1974. The Miocene Caribbean Faunal Province and its Subprovinces. Verhandlungen der naturforschenden Gesellschaft in Basel 84(1):209–213.